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Agave evolution and taxonomy

Jiménez-Barron, O, García-Sandoval, R, Magallón, S, García-Mendoza, A, Nieto-Sotelo, J, Aguirre-Planter, E & Eguiarte, L E (2020) Phylogeny, diversification rate, and divergence time of *Agave* sensu lato (Asparagaceae), a group of recent origin in the process of diversification. *Frontiers in Plant Science* 11: 1–17.

doi: 10.3389/fpls.2020.536135

Agave is a large and diverse genus of North and Central American and Caribbean succulents with around 250 species, which often form dominant components of many arid ecosystems. These plants are popular with growers for their architectural appearance, but many can take two to three decades to reach flowering size, even under optimal growing conditions. Most, but not all, die after flowering.

The first studies of *Agave* evolution based on molecular evidence were published 25 years ago (Bogler & Simpson, 1996). This current paper by Jiménez-Barron et al (2020) is the most important to date providing additional support to earlier proposals, but it also further advances our understanding of how agaves have evolved. This field of study under review is new and termed *phylogenomics*: the interaction between studies of evolutionary history (*phylogenetics*) and the molecular sequencing of genes (*genomics*). The aim is to trace evolutionary pathways based on comparative gene sequencing data, so that the resulting taxonomy should truly reflect the evolutionary interrelationships within and between plant families, genera and species.

This latest study contains many valuable insights into the evolutionary history of *Agave* and its close relatives, particularly in terms of major diversification events. Here I summarise key features and their possible future impacts on the taxonomy.



Fig. 1 *Agave bracteosa*, now shown to exhibit primitive features compared to the rest of the genus (Photo: Colin Walker)



Fig. 2 *Agave stricta* is a typical member of Section *Juncineae* characterised by having numerous hard, long, thin, dagger-like leaves (Photo: Colin Walker)

- *Agave bracteosa* is shown to be basal and hence most primitive compared to the rest of *Agave*. This confirms my long-held view that this species is unusual. It branches freely to form large clumps (Fig. 1), its leaves are very brittle, curling and unarmed, as opposed to the very tough, fibrous leaves of typical agaves which often have fierce teeth and spines. Most importantly *A. bracteosa* produces multiple inflorescences, often consecutively but not necessarily simultaneously, so after an initial flowering the rosette and hence the plant does not die. Such a strategy is termed 'iteroparous', characterised by multiple reproductive cycles over the course of a lifetime. This contrasts to the single flowering event of a rosette of say *Agave victoriae-reginae* which is followed by death, an alternative strategy referred to as being 'semelparous'.
- A group of 11 species is confirmed as being distinctive, forming another early and hence old branch in the *Agave* evolutionary family tree. Plants consist of rosettes with numerous long, narrow, hard leaves with dagger-like sharp terminal spines (Figs. 2 & 3). Taxonomically this group is currently recognised as Section *Juncineae* (formerly group *Striatae*).



Fig. 3 *Agave albipilosa* is an atypical member of Section *Juncineae* with leaves bearing clusters of fine white hairs, the function of which is currently unknown. Plant in the collection of Tina Wardhaugh (Photo: Colin Walker)

- Bogler & Simpson (1996) were the first to show that the separate genera *Manfreda*, *Polianthes* and *Prochnyanthes* were nested within and hence not distinct from *Agave*. These c.40 species were subsequently transferred to *Agave*.
- An unexpected result is that the very attractive *Agave pelona* sits in a branch (clade) currently by itself.
- The rest of *Agave* species then form one large, closely interrelated clade but the resolution of their relationships is not currently clear.
- A significant consequence of this study is that the division of *Agave* into three subgenera does not appear to reflect their evolutionary history. Subgenus *Manfreda* does form a distinct branch, but the two other subgenera *Agave* and *Littaea* are not monophyletic, ie members of each do not form a single unit with a common evolutionary origin. So, for example, members of subgenus *Littaea* namely Section *Juncineae* are separated from *A. bracteosa*, the filiferous agaves: *A. filifera*, *A. schidigera* and allies (Walker, 2020), *A. pelona*, *A. victoriae-reginae* and other species that produce unbranched flower spikes.
- Finally for *Agave*, *A. sisalana* and *A. tequilana*, the two most economically important species, are shown to be very closely related and are apparently the most evolutionarily advanced (but it is possible that selection and hybridisation under cultivation over many centuries may account for this result).
- Now on to the close relatives of *Agave*. *Hesperoyucca whipplei* with unique features such as bulb formation in its seedling stage (a feature absent from true species of *Yucca*), is confirmed as being only distantly related

to all the other yuccas, but is sister to, hence very closely related to, the genus *Hesperaloe*.

- Finally, the genera *Beschorneria* and *Furcraea* are apparently not the distinct, separate entities as currently circumscribed.

LITERATURE:

Bogler, D J & Simpson, B B (1996) Phylogeny of Agavaceae based on ITS DNA sequence variation. *Amer. J. Bot.* **83**(9): 1225–1235.

Walker, C C (2020) Filiferous agaves. *CactusWorld* **38**(1): 41–48.

C C Walker

A review of the *Euphorbia schinzii* complex in southern Africa

Bruyns, P V, Klak, C & Hanáček, P (2020) A review of the *Euphorbia schinzii*-complex (Euphorbiaceae) in southern Africa. *Phytotaxa*, **436**(3): 201–221.

doi.org/10.11646/phytotaxa.436.3.1

The species closely related to *Euphorbia schinzii* (subgenus *Euphorbia*) are reviewed for southern Africa. These 11 species are distributed across southern Angola, northern Namibia, Botswana, Zimbabwe, north-east South Africa, Swaziland (Eswatini) and southern Mozambique. They are characterised by having short, thin spiny branches that often clump freely to form large clusters. The only species commonly cultivated is *E. aeruginosa*, which is deservedly very popular for its distinctive and attractive pale blue-green colour resembling weathered copper, hence its name (Fig. 4).

Euphorbia schinzii, the most widely distributed species of this group, now consists of three subspecies: subsp. *schinzii* with a limited range in east South Africa and Eswatini; subsp. *bechuanica* (formerly *E. malevola* subsp.



Fig. 4 *Euphorbia aeruginosa* in cultivation (Photo: Colin Walker)



Fig. 5 *Euphorbia schinzii* subsp. *schinzioides* growing in its typical habitat amongst grass and rocks, northern Pretoria, photographed in 2007 (Photo: Colin Walker)

bechuanica and now including *E. limpopoana* as a synonym) is widely distributed in Zimbabwe, Botswana, northern South Africa and south-east Mozambique; subsp. *schinzioides* is newly described from the Mpumalanga Province of South Africa. The last named is the only member of this group that I have seen growing in habitat in 2007 (Fig. 5) at what was then considered to be the type locality for *E. schinzii*.

Other species treated are: *E. clivicola* (extended to include collections from a wider area, including the new subsp. *calcritica*), *E. kaokoensis*, *E. louwii*, *E. lydenburgensis*, *E. otjipembana* (with the new combination subsp. *fluvialis*), *E. subsalsa* and *E. venteri*. Two new species are described. *Euphorbia pisima* is localised in the Limpopo Province of South Africa and is characterised by forming dense clumps of bright pea-green branches, hence its name. *Euphorbia steelpoortensis* (from the Steelpoort District, Limpopo Province, South Africa) is most closely related to *E. aeruginosa*, *E. pisima* and *E. lydenburgensis*.

This paper is well illustrated with detailed distribution maps, habitat photos, a figure comparing the branch morphology across a range of taxa and detailed line drawings.

Colin C Walker

Extrafloral nectaries in *Aloe* – the sequel

In the September 2019 issue of *CactusWorld* I reported the presence of extrafloral nectaries (EFNs) on the fruits of the hybrid *Aloe* 'Hanky Panky' (*A. dhufarensis*, *A. jucunda*). Together with *A. citrina* these were the only records so far of such nectaries in the genus (Jonkers, 2018). Since EFNs were not observed in the maternal parent (*A. dhufarensis*) I asked growers of *A. jucunda* to pollinate their plants and look for signs of nectar on the fruits.

I am most grateful to Ian Eckford (Highbury, London N5) who on 20 October 2020 sent the following report, "With reference to your article ... this year the fruits on my plant of *Aloe jucunda* all bore nectar droplets, which were replaced by more droplets within 15 minutes of my wiping them away. Nectar was also noticed on the fruits of *A. somaliensis* ...". He added that the plants were open-pollinated in his greenhouse. So, Ian can be credited not only for his confirmation of *A. jucunda* being the species from which the EFNs were inherited, but also for recording a third *Aloe* with EFNs.

In the evolutionary tree of Grace et al (2015), based on molecular DNA analysis, *A. jucunda*, *A. somaliensis* and *A. trichosantha* (the closest relative of *A. citrina*; Carter et al, 2011) are part of a (sub-)clade chiefly consisting of north-east African and Socotran species. For experimentally inclined growers it might be a challenge to investigate if there are more species with EFNs within this assembly. Good candidates would be the smaller floriferous species, such as the very free-flowering *A. jacksonii* (Walker, 2017).

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Fig. 6 *Aloe jacksonii* (Photo: Colin Walker)



Fig. 7 *Lithops* 'Black Top' (Photo: Andy Yang)

New *Lithops* cultivar registrations 2020

Nine new epithets were added to the official cultivar register of *Lithops* N.E.Br. during 2020, seven of which originated in China. The full up to date register can be viewed and downloaded from:

<http://www.scrapbooklithops.com/cultivars.html>



Fig. 8 *Lithops* 'Chinchillas ZW' (Photo: Zhang Shijia and Wei Zichu)

'Black Top'

L. lesliei subsp. *lesliei* var. *venteri* 'Black Top'. First published by Andy Yang in "Andy's *Lithops* Handbook 2021: 81. 2020". Image example: photograph accompanying the protologue taken by Andy Yang of Yuxi City, China. This appears to be an intensification of the well know *maraisii* form and has appeared on seed lists previously, although without formal description. It is likely much of the material



Fig. 9 *Lithops* 'Halo' (Photo: Bernd Schlosser)

available today was bred by Steven Hammer and first released on the Mesemb Study Group seed list in 2011 as MSG 2598. A stabilised var. *venteri* with a wide open dark face. (The polar opposite of var. *venteri* 'Pepper Pot' as documented below.)

'Chinchillas ZW'

Lithops 'Chinchillas ZW'. First published by Zhang Shijia and Wei Zichu as, A new pattern cultivar: *Lithops* N.E.Br. 'Chinchillas ZW', in *Mesemb Study Group Bulletin* 35(2): 45 (May, 2020). Image example: six photographs accompanying the protologue, figures 33.62–33.67 on page 44, taken by the authors. A rounded, delicately patterned hybrid of unknown parentage, with a grey to purple colouration and yellow flowers. The epithet honours two pet Chinchillas.

'Halo'

Lithops aucampiae subsp. *aucampiae* var. *aucampiae* 'Halo'. First published by Bernd Schlösser as, *Lithops aucampiae* subsp. *aucampiae* var. *aucampiae* 'Halo', in *Avonia* 38(4): 328–329 (December, 2020). Image example: photograph 1, accompanying the protologue, taken by Boris Rommer of Germany. A cultivar with wide-open brown to mauve windows and narrow margins. (This form has previously been traded under various unpublished titles including 'corona', which since the current pandemic could potentially be regarded as an offensive epithet.)

'Lindsey Deaves'

Lithops coleorum 'Lindsey Deaves'. First published by Terry Smale as, 'Foggy Dew' and 'Lindsey Deaves', two new mesemb cultivars, *Cactus World* 38(4): 292 (December, 2020), originating from Lindsey Deaves of Leatherhead, UK. Nomenclatural standard: photograph Fig. 3 accompanying the protologue taken by Terry Smale of Epsom Downs, UK. A cultivar with an overall purple or pinkish flush. The epithet honours the late Lindsey Deaves.



Fig. 10 *Lithops* 'Lindsey Deaves' (Photo: Terry Smale)



Fig. 11 *Lithops* 'Nine Rivers ZW' (Photo: Zhang Shijia and Wei Zichu)



Fig. 14 *Lithops* 'Sunny Grassland ZW' (Photo: Zhang Shijia and Wei Zichu)



Fig. 12 *Lithops* 'Pepper Pot' (Photo: Andy Yang)



Fig. 13 *Lithops* 'Spotted Dog' (Photo: Andy Yang)

'Nine Rivers ZW'

Lithops julii 'Nine Rivers ZW'. First published by Zhang Shijia and Wei Zichu as, A new pattern cultivar: *Lithops* N.E.Br. 'Nine Rivers ZW' in *Mesemb Study Group Bulletin* 35(1): 2020 (February, 2020). Image example: Six photographs accompanying the protologue, figures 35.26–35.31 on page 3 taken by Zhang Shijia and Wei Zichu of China. A yellow-green cultivar with carved-effect borders and lip smears. The epithet honours the Chinese Emperor Yu who had nine rivers dug to avert a great flood, around 2000 BC. The authors state that the photographs do not do these plants justice and they really need to be seen in the flesh for the three-dimensional effect to be fully appreciated.

'Pepper Pot'

Lithops lesliei subsp. *lesliei* var. *venteri* 'Pepper Pot'. First published by Andy Yang in *Andy's Lithops Handbook 2021*: 81 (2020). Image example: photograph accompanying the protologue taken by Andy Yang of Yuxi City, China. A stabilised var. *venteri* with multiple small dark spots on a light face. (The polar opposite of var. *venteri* 'Black Top' as documented above.)

'Spotted Dog'

Lithops. aucampiae subsp. *euniceae* var. *fluminalis* 'Spotted Dog'. First published by Andy Yang in *Andy's Lithops Handbook 2021*: 79 (2020). Image example: photograph accompanying the protologue taken by Andy Yang of Yuxi City, China. The epithet is the name of an English pudding famed for its dotted appearance. A stabilised var. *fluminalis* of elliptical shape that is festooned with intricate dots and dashes all over the face. The base colour is brown and the characteristic var. *fluminalis* marginal peninsulas are not as distinct.



Fig. 15 *Lithops* 'Voldemort's Visage' (Photo: Jie Shen)

'Sunny Grassland ZW'

Lithops divergens var. *amethystina* 'Sunny Grassland ZW'. First published by Zhang Shijia and Wei Zichu as, A new aberrant colour form pattern cultivar: *Lithops* N.E.Br. 'Sunny Grassland ZW' in *Mesemb Study Group Bulletin* 35(3): 66 (September, 2020). Image example: four photographs accompanying the protologue, figures 35.101–35.104 on page 67, taken by the authors. A bright green cultivar with a pale facial stippling.

'Voldemort's Visage'

Lithops olivacea var. *olivacea* 'Voldemort's Visage'. First published by Jie Shen as, Voldemort's Visage in *Mesemb Study Group Bulletin* 35(3): 66 (September, 2020). Image example: four photographs accompanying the protologue figures 35.97– 5.100 on page 52, taken by Jie Shen of China. Some minor spelling and format errors in the article as published were corrected for the register. A cultivar with reduced windows, a grey-green or light brown colour and a deep fissure. The epithet is the name of the misshapen and wicked Voldemort character in the Harry Potter novels.

NB Andy's *Lithops Handbook 2021*, mentioned above, was actually published before the end of 2020.

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Halting plant extinction webinar (November 2020)

Recent analysis by Humphreys et al (2019) showed that plant extinction is 500 times higher than it was over 200 years ago, so there is now a race against time to save plant biodiversity.

In order to explore and discuss the current extinction crisis in plant biodiversity, the Royal Botanic Garden, Edinburgh,

and the Royal Society of Edinburgh jointly hosted a webinar event on 26 November 2020. This event, originally planned as a face-to-face meeting but switched to online for obvious reasons, attracted an incredibly large worldwide audience of around 750 stakeholders and lasted for just an hour.

The webinar was co-chaired by Dr Julieth Serrano (Postdoctoral researcher at *Bioresilience*) and Professor Peter Hollingsworth FRSE (Director of Science at the Royal Botanic Garden, Edinburgh).

The prestigious discussion panel consisted of four biodiversity and conservation specialists, representing leaders and front-line workers in the global plant conservation effort:

- Professor Jin Chen (Xishuangbanna Botanic Garden, China)
- Professor Sandra Díaz (National University of Córdoba, Argentina)
- Professor Corneille Ewango (University of Kisangani, Democratic Republic of the Congo)
- Dr Malin Rivers (Head of Conservation Prioritisation, *Botanic Gardens Conservation International*).

The panel members views of the future for plant conservation were explored. Key areas were covered such as whether zero extinction is achievable, the balance between species and habitat-based conservation programmes and how botanic gardens can make a long-term contribution to preventing extinction. These questions and more were explored using examples of success and failure at all stages of the conservation journey.

Here I highlight some of the issues raised using case studies featuring *Aloe* and its close relatives. As most readers will be aware, this genus is currently protected by CITES regulations, but this deals only with trade in aloes and aloe products. This is a particularly difficult issue because *Aloe vera*, and to a lesser extent *Aloe ferox*, are the basis of multi-billion dollar cosmetic and toiletry industries, such that other endangered aloes can readily be traded under false identities. Distinguishing between *A. vera* and many other species often requires specialist knowledge.

Humphreys et al (2019) examined the geographical pattern of modern extinction in seed plants and concluded that, "Hawaii stands out as having the most recorded extinctions (79), followed by the Cape Provinces of South Africa (37) and Mauritius (32), with Australia, Brazil, India and Madagascar also being among the top regions". Of these countries, aloes are native to Madagascar, South Africa and Mauritius, so here I discuss the conservation and extinction crises of three aloes native to the first two countries.

The plight of the Madagascan endemic *Aloe bakeri* has already been highlighted here (Walker, 2019). In summary, it is not trade but habitat destruction caused by human development that has pushed this small, highly localised species to the brink of extinction. My assessment



Fig. 16 *Aloestrela* (*Aloe*) *suzannae*, near Itampolo, south-west Madagascar (Photo: Al Laius)

was that it is either *Critically Endangered* (CR) or even *Extinct in the Wild* (EW) on the basis of IUCN criteria. This species, though, is easy to propagate and hence is fairly common in cultivation. However, the unresolved conundrum is that trade of cultivated material is actually prohibited under CITES regulations! Regrettably I suspect that an outcome of a full, habitat-based assessment in the near future could confirm this species as having the status of EW.

A second endangered Madagascan endemic is *Aloestrela* (formerly *Aloe*) *suzannae* (Fig. 16). This species has long been recognised as unique from its morphological features, notably the white to creamy-white nocturnally-opening scented flowers. It is the largest of the Madagascan aloes with stems up to 4m (possibly even up to 7m) tall with slender unbranched flower spikes up to 3m tall. On the basis of recent molecular studies this species was shown to form an ancient, early-branching lineage and consequently was separated from *Aloe* as the monotypic *Aloestrela suzannae* (Smith & Molteno, 2019). It occurs in the Toliara Province of Madagascar, where it has a restricted and fragmented range with only relatively small numbers of individuals remaining due to agricultural development. It has been assessed as being *Critically Endangered*. As a consequence of its large size (unlike the dwarf *A. bakeri*) this species does not make an attractive plant for cultivation under small greenhouse conditions in America and Europe. This species is therefore relatively uncommon in cultivation. Continued, uncontrolled development could easily push this species into extinction (EW).

The final case study is of the South African species, *Aloe lettyae*. The recent study by Kremer-Köhne et al (2020) is the first to document the distribution and population biology of this *Endangered* species. *Aloe lettyae* is a maculate (spotted-leaved) species endemic to the highly threatened Woodbush Granite Grassland in the Limpopo Province of South Africa. Just 19 populations were documented and the total area of occupied habitat was calculated to be 17.5ha within its extent of occurrence of 123km². The total number of individuals was estimated to be only c.10,800. This study provides the baseline data for the long-term monitoring which will aid management and conservation of what is described as “the range restricted *Endangered* *A. lettyae*”. Currently it is unknown if *A. lettyae* populations are increasing or declining, hence the need for long-term monitoring. The authors hope that *A. lettyae* can “be used as a flagship species in raising support for the conservation of its highly threatened habitat”.

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- Colin C Walker



Fig. 17 Inflorescence of *Aloestrela* (*Aloe*) *suzannae*, near Itampolo, south-west Madagascar (Photo: Al Laius)